

COLOR PATTERNS OF SPINNER PORPOISES
(*STENELLA* CF. *S. LONGIROSTRIS*) OF THE EASTERN PACIFIC
AND HAWAII, WITH COMMENTS ON DELPHINID PIGMENTATION

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ABSTRACT

In this paper, the second of a series on the morphology of small pelagic delphinids by the author, the color patterns of forms of a tropical spinner porpoise *Stenella* cf. *S. longirostris* (Gray) 1828 from the far eastern Pacific, from the waters between North America and Hawaii, and from Hawaiian waters are described and illustrated. The patterns can be analyzed in terms of discrete component systems, and most geographical variation appears to be in a "dorsal field system" overlying a basic general pattern. The overlay is darkest and most extensive in the easternmost form considered and lightest and least extensive in the Hawaiian form. The color patterns of three other delphinids, *Stenella graffmani*, *Delphinus* sp., and *Tursiops truncatus* are analyzed with the component approach, and possible pattern element homologies are defined.

During the course of collecting materials and data for population studies of porpoises involved in the seine fishery for tunas in the eastern tropical Pacific (Perrin, 1970a), I have during the last several years had the opportunity to observe and, less often, to photograph the color patterns of a large number of small pelagic delphinids of several species. Emerging patterns of variation and their possible implications for the systematics of these very poorly known mammals have prompted me to undertake detailed analyses of this body of observations. I have previously (Perrin, 1970b) described the color pattern of the eastern Pacific spotted porpoise *Stenella graffmani* (Lönnerberg) 1934. The primary purpose of this paper is to describe the ontogeny and geographical variation of the color patterns of spinner porpoises of the eastern tropical Pacific and Hawaii. Some description is included

also of variation in the shape of the dorsal fin and correlated features.

The study is based on observations on 157 specimens from the eastern Pacific (Figure 1), of which 41 were photographed, and on photographs and observations of approximately 35 wild and captive animals from Hawaiian waters. Many of the specimens, including most of those from the far eastern Pacific east of Clipperton Island, were examined minutes after capture; others were examined after being held in frozen storage for up to 8 months. Degree of sexual development was determined by histological examination of gonads, with the exception of the large male (Figure 8) from Acapulco, of which only a photograph is available and which was undoubtedly a mature male. Skeletons of specimens of many of the animals illustrated were placed in museums, and the museum numbers are given in the figure captions.

The spinner porpoise of the far eastern Pacific has been referred to *Stenella microps* (Gray) 1846 (Miller and Kellogg, 1955; Hester,

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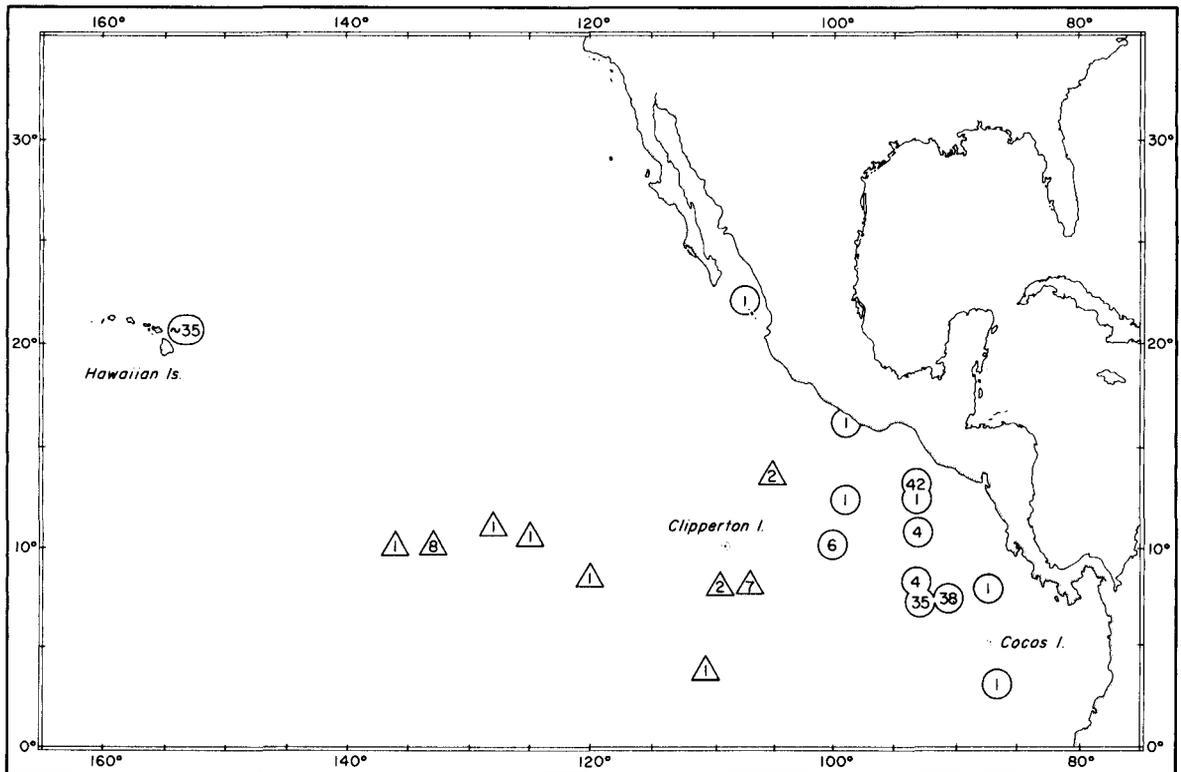


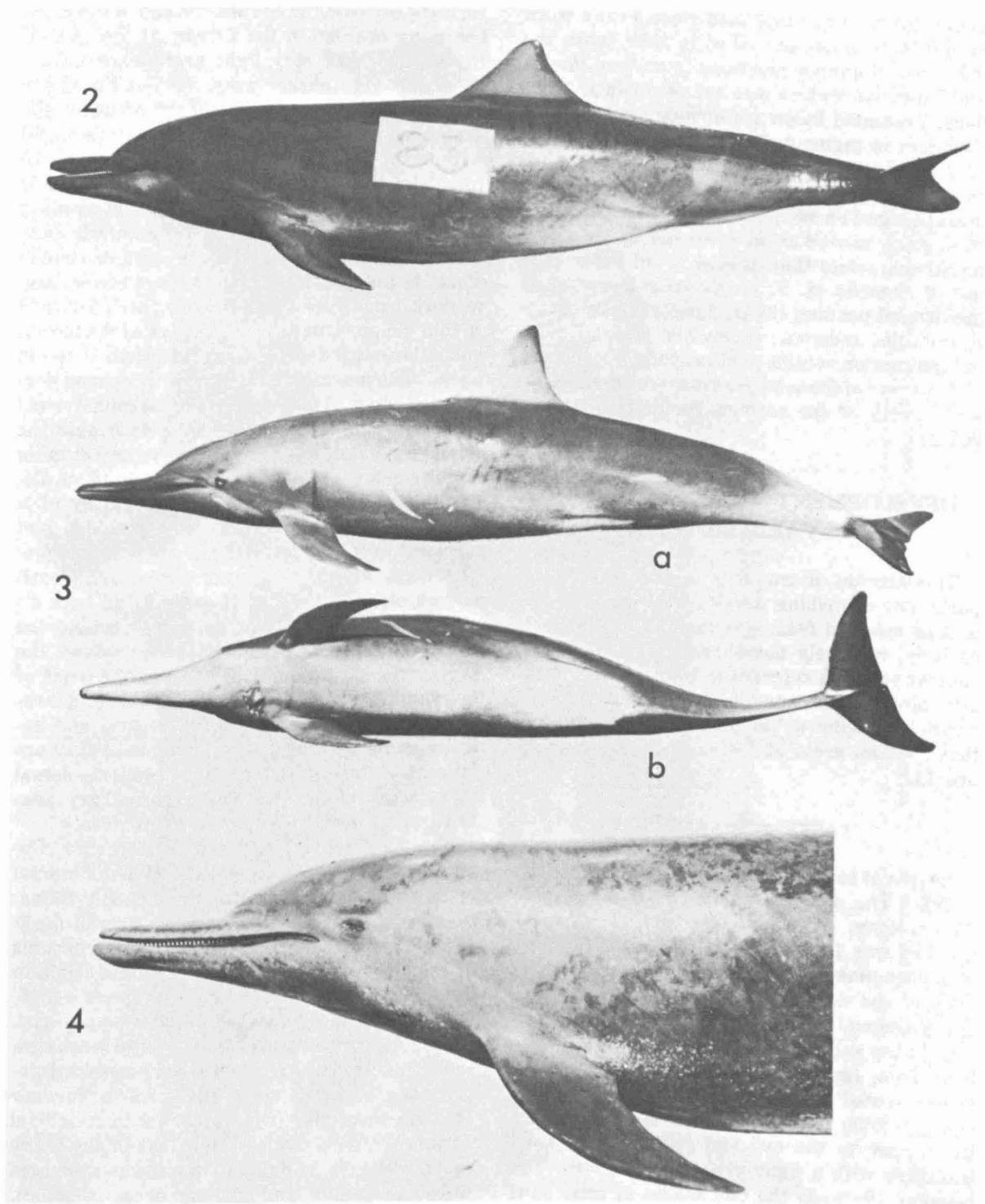
FIGURE 1.—Localities and numbers of specimens examined. Circles in eastern area indicate “eastern spinners”; triangles indicate “whitebelly spinners.”

Hunter, and Whitney, 1963; Nishiwaki, 1967; Pilson and Waller, 1970), but others regard *S. microps* as a synonym of *S. longirostris* (Gray) 1828 (Hershkovitz, 1966; Rice and Scheffer, 1968; Harrison, Boice, and Brownell, 1969). The spinner porpoise of Hawaii has been referred to *S. longirostris* (Hershkovitz, 1966; Nishiwaki, 1967; Tomich, 1969) and to *S. roseiventris* (Wagner) 1853 (Brown, Caldwell, and Caldwell, 1966; Fraser, in Morris and Mowbray, 1966; Rice and Scheffer, 1968). The type localities for *S. microps* and *S. longirostris* are unknown; *S. roseiventris* was described from the Banda Sea, Indonesia. The spinner porpoise of the far offshore areas of the eastern Pacific—called “whitebelly spinner” by fishermen—has not to my knowledge been previously described or referred to any named species. No critical review of the

FIGURE 2.—Calf of eastern spinner. Male, 105 cm total length, from lat 10°30'N, long 92°56'W, April 4, 1968. Perrin field no. CV83; specimen not saved. Shape of dorsal fin is distorted by angle of photograph, should be higher. Photographed minutes after death.

FIGURE 3.—Lateral (a) and ventral (b) views of subadult eastern spinner. Female, 166 cm, from 21°43'N, 106°47'W, February 17, 1967. Marine Mammal Biological Laboratory (Seattle) field no. 1967-102. Skeletal specimen in MMBL collection. Photographed minutes after death.

FIGURE 4.—Adult eastern spinner. Female, 166 cm, from 12°51'N, 93°18'W, April 9, 1968. Perrin field no. CV7; specimen not saved. Photographed minutes after death.



genus has been accomplished since True's work on the Delphinidae published in 1889, when the existence of spinner porpoises in eastern Pacific and Hawaiian waters was not yet known. Evidence presented below concerning geographical variation in pigmentation supports the concept of a single species, highly variable geographically, but taxonomic and nomenclatorial decisions must be based on adequate review of osteological characters, as well as on a broader range of external characters than is considered here. The use of *Stenella* cf. *S. longirostris* therefore is provisional pending the outcome of more extensive studies underway by me and others. A similar situation obtains for the spotted porpoises, and use here of *Stenella graffmani* for the spotted porpoise(s) of the eastern Pacific is also provisional.

DEVELOPMENT AND INDIVIDUAL VARIATION

This account of ontogeny is divided into two parts, one describing development of color pattern as inferred from specimens from the more easterly, relatively nearshore population(s) of spinner porpoise referred to below as the "eastern spinner," and another for specimens of the "whitebelly spinner" of the more westerly, farther offshore areas of the eastern Pacific (Figure 1).

EASTERN SPINNER

Length at birth is 75 to 85 cm (Harrison et al., 1969). The smallest specimen examined was 80 cm long. The smallest specimen photographed was 105 cm long (Figure 2). At this size, the animal is predominantly dark gray. The gray of the dorsum grades imperceptibly into white around the genital region and in a smaller area in the axillary region. A dark gray flipper band from flipper base to the eye-gape region is demarcated above by a narrow, very light line running from behind the posterior insertion of the flipper to the eye and below by a sharp boundary with a light gray gular region. The boundary between the two shades of gray runs

forward between the eye and the end of the gape, becoming obscure in the furrow at the base of the melon. The very light gray below grades anteriorly into darker gray, so that the upper and lower sides of the snout are of about the same shade as the dorsal field. The gape is edged with very dark gray sharply delineated above for about the last third of the gape and below for about the last half of the gape but grading distally above and below into the generally dark gray of the snout. A small eye patch of similar shade is present, and a narrow eye stripe, also of dark gray, runs from the eye patch forward to join the gape mark near the apex of the melon. A similar mark extends from the blowhole to the apex. The margin of a very faintly defined dorsal cape (not visible in the photographs) runs from near the apex of the melon to behind the dorsal fin, passing high over the eye and dipping slightly below the fin to yield a saddle effect discernible only upon very careful scrutiny of a freshly caught animal. Low on the side and adjacent to the genital slit, an elongate, smudge-like mark extends obliquely for several centimeters along a line that if extended in both directions would run from the eye to behind the anus. All appendages are on both surfaces the same gray as the dorsum. The major point of individual variation in animals of this and larger size is in the extent of the ventral and axillary white areas; in some individuals they are larger and may even be confluent, with the dorsal margin extending back from the axillary area to run into the higher genital white area.

The pattern persists as described into subadulthood (subadult being defined as an animal of adult or near-adult size but sexually immature) without change aside from overall darkening (Figure 3). In subadulthood the margins of the ventral and axillary white areas begin to become speckled, and in adults (Figures 4, 5, 6, 7, 8, and 9) the dorsal field, by now very dark gray, appears to encroach on the white areas with spots and blotches to yield a very speckled appearance below (Figure 10). As in younger animals, the major feature subject to individual variation appears to be the extent of the white areas, although in no adult specimens examined were the genital and axillary areas confluent.

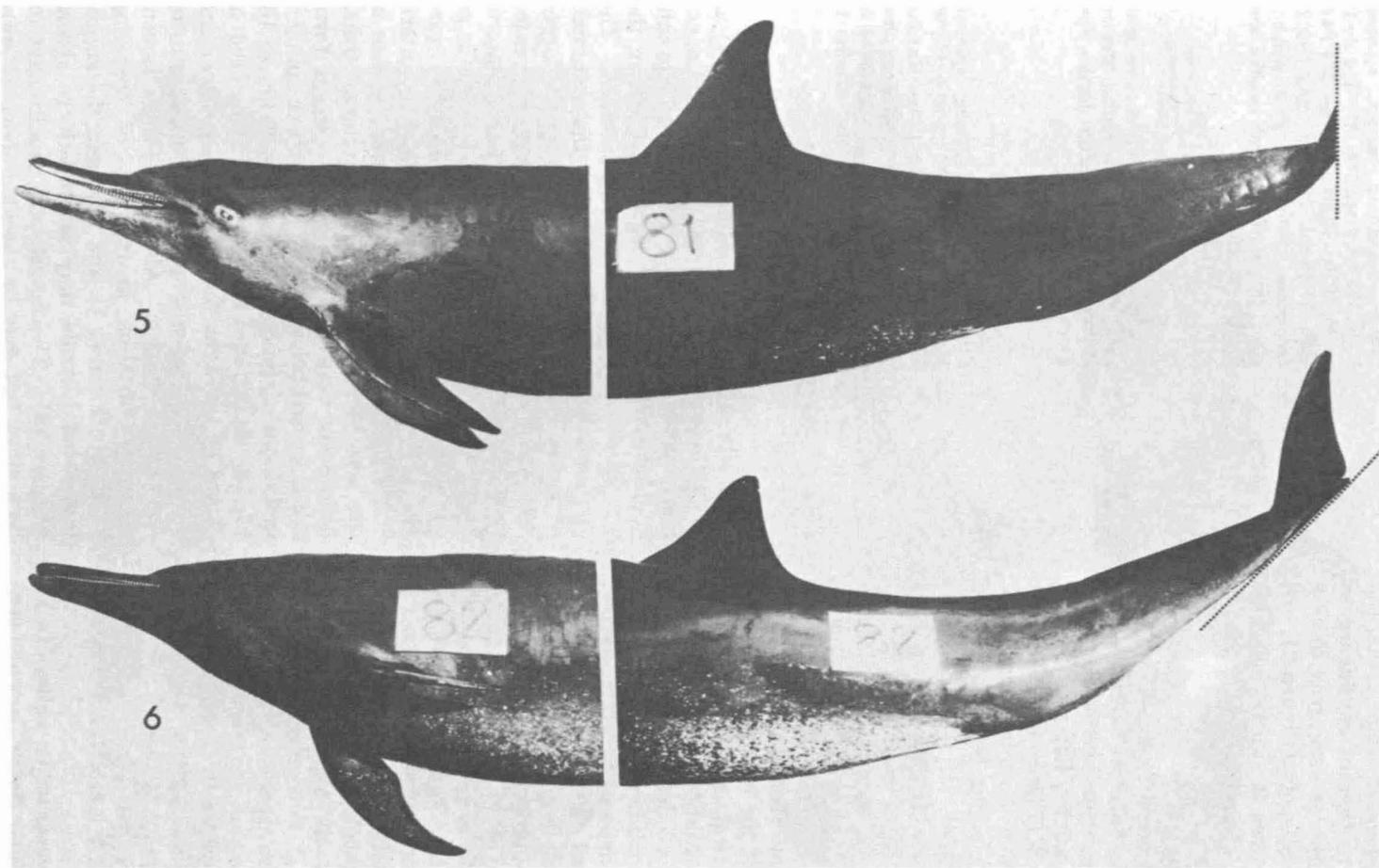


FIGURE 5.—Adult eastern spinner. Female, 160 cm, from $10^{\circ}30'N$, $92^{\circ}56'W$, April 12, 1968. Perrin field no. CV81; specimen not saved. Photographed minutes after death.

FIGURE 6.—Adult eastern spinner. Female, 169 cm, from $10^{\circ}30'N$, $92^{\circ}56'W$, April 12, 1968. Perrin field no. CV82; specimen not saved. Photographed minutes after death.

In the specimens with largest white areas, the region corresponding to that of confluence in some younger specimens was dark gray thickly peppered with light gray spots (Figure 6). In some adults, the gular area is also flecked with light spots (Figure 4). In all adults the degree of contrast between the flipper band and the gular region is much reduced over that in younger animals. The cape remains obscure (see photograph of specimens in water in Perrin, 1968). The oblique mark adjacent to the genital region is obliterated in most adults, but in some can still be faintly discerned (Figure 6). The thin light gray line delineating the upper margin of the flipper band may in adults be prominent or so faint as to appear absent.

In adult males, the dorsal fin is canted forward to a greater or lesser degree (Figures 7, 8, and 9). Development of this feature is correlated with development of a protuberant keel, composed of connective tissue, just posterior to the anus. The function of these features is unknown. However, comparison of the habits of this spinner with those of the Hawaiian spinner, in which the features are very weakly developed (see below), provides a basis for a deductive hypothesis. In the eastern Pacific, spinners commonly occur together with spotted porpoise (*S. graffmani*) in mixed schools comprised of several hundred, or even thousands, of individuals of each species. In Hawaiian waters, spinners and spotted porpoise [there referred to *S. attenuata* (Gray)] do not occur in mixed schools (personal communication from K. S. Norris). In Hawaiian waters, then, most interspecific contacts could be assumed to be head-on and made at some distance, while in the mixed schools of the eastern Pacific interspecific contacts must be relatively more frequent, made at shorter distances, and for the most part lateral. It can be hypothesized that the features function in species recognition in a sexual context, perhaps, for example, to insure that oestrous females make advances to males of the proper species.

WHITEBELLY SPINNER

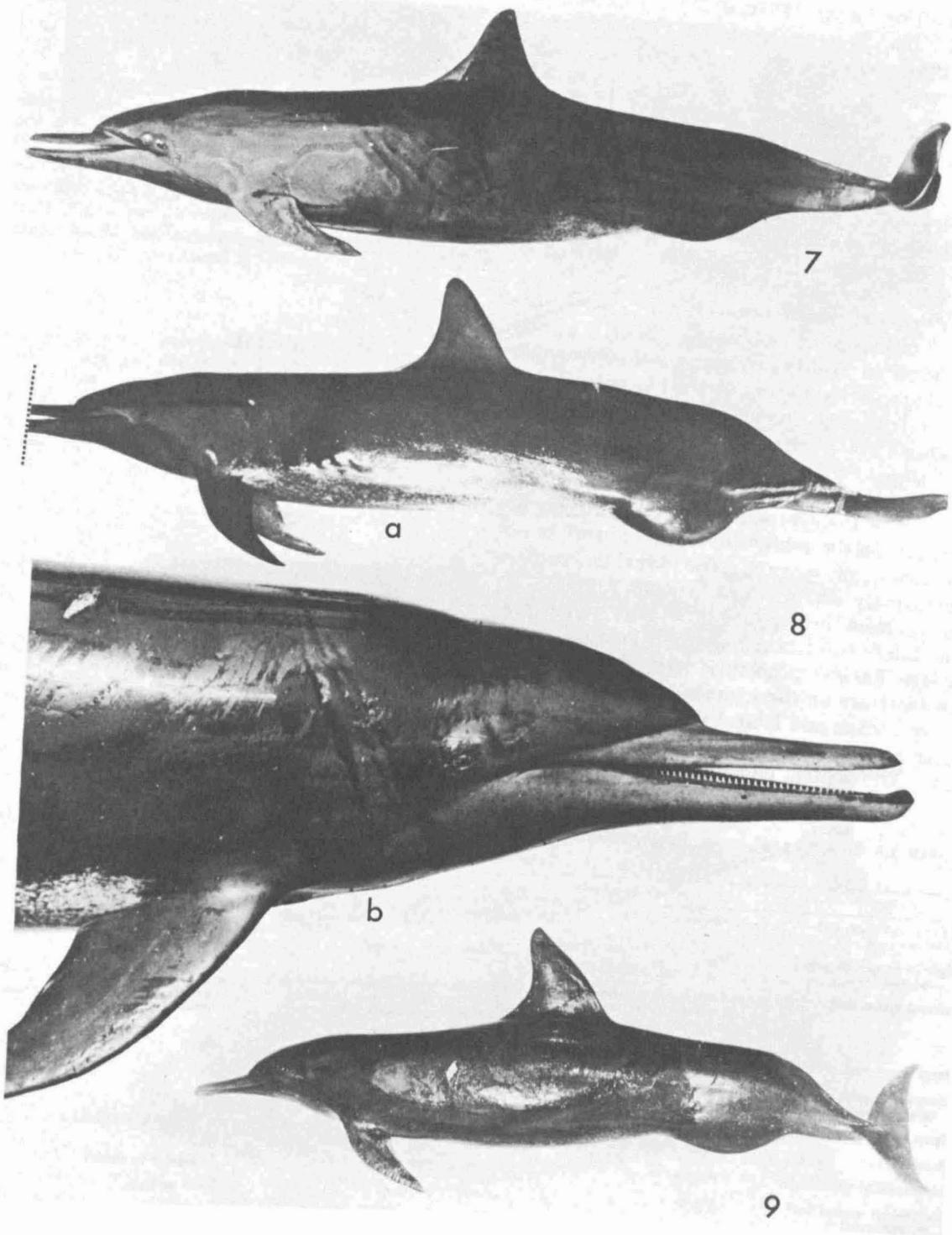
In this animal the ventrum is white. In all young specimens examined, the axillary and gen-

FIGURE 7.—Adult eastern spinner. Male, 175 cm, from 3°N, 87°W, July 19 or 20, 1970. Perrin field no. WFP47; U.S. National Museum no. 396026 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 8a and b.—Adult eastern spinner. Male from off Acapulco, Mexico. Photographed soon after death. Specimen not saved.

FIGURE 9.—Adult eastern spinner. Male, 186 cm, from 12°20'N, 92°53'W, March 10, 1968; San Diego Natural History Museum no. 21427 (complete skeleton and cast). Photographed in frozen state after several months in frozen storage.

ital white regions were confluent (Figure 11) as in only some young eastern spinners. Again, not much change occurs in the pattern until late subadulthood (Figures 12, 13, and 15) when the margin of the ventrum becomes speckled. The main point of difference between these animals and the eastern specimens, aside from the larger ventral light areas, is that there is much greater contrast between the dorsal cape and the lateral field. The cape can even be discerned in some of the photographs of frozen specimens (Figure 13). In some subadults (Figure 13) an anteriorly narrowing dark gray mark can be seen in the area between the flipper insertions. Other differences between this and the eastern form are discussed below. As in the eastern spinner, individual variation among adults (Figures 16, 17, 18, 19, 22, and 23) is most pronounced in extent of the light ventrum, but the lower end of the range is about equal to the upper end for the eastern spinner. Also again, there is considerable variation in intensity of speckling (compare Figures 16 and 22), and the supra-flipper-band stripe may be effectively absent (Figure 19). The flippers are usually dark on both sides, but may be speckled above (Figure



22) and/or below (Figure 21). The oblique mark adjacent to the genital region is obliterated in some adults, but in others (Figure 23) is very clearly delineated.

GEOGRAPHICAL VARIATION

Very young specimens of the Hawaiian spinner (Figure 24, and Figure 7 in Perrin and Hunter, 1972) were not available for examination nor was it possible to determine with certitude the degree of maturity of most of the animals seen. One large male observed (PUKA at Sealife Park in Waimanalo, Oahu), however, has been in captivity for 5 years and can be presumed to be adult. The major differences between the Hawaiian spinner and the whitebelly spinner of the eastern Pacific are that in the Hawaiian animal the light ventrum extends dorsad nearly to the level of the eye, as it does in its extreme expression in the whitebelly spinner, and is not speckled at the margin. The dorsal fin becomes increasingly erect with development, but is always at least slightly falcate, and the ventral keel associated with triangular and canted fins in the eastern Pacific spinners is all but absent. All contrasts are on the average more pronounced: between cape and lateral field, flipper band and gular area, gape mark and underside of lower jaw. The ventral margin of the cape follows a

FIGURE 10.—Close view of genital region of adult male eastern spinner depicted in Figure 9.

FIGURE 11.—Lateral (a) and ventral (b) views of calf of whitebelly spinner. Female, 105 cm, from 8°N, 109°45'W, March 5, 1969. Perrin field no. PQ11; U.S. National Museum 395601 (complete skeleton). Photographed frozen after approximately 1 month in frozen storage.

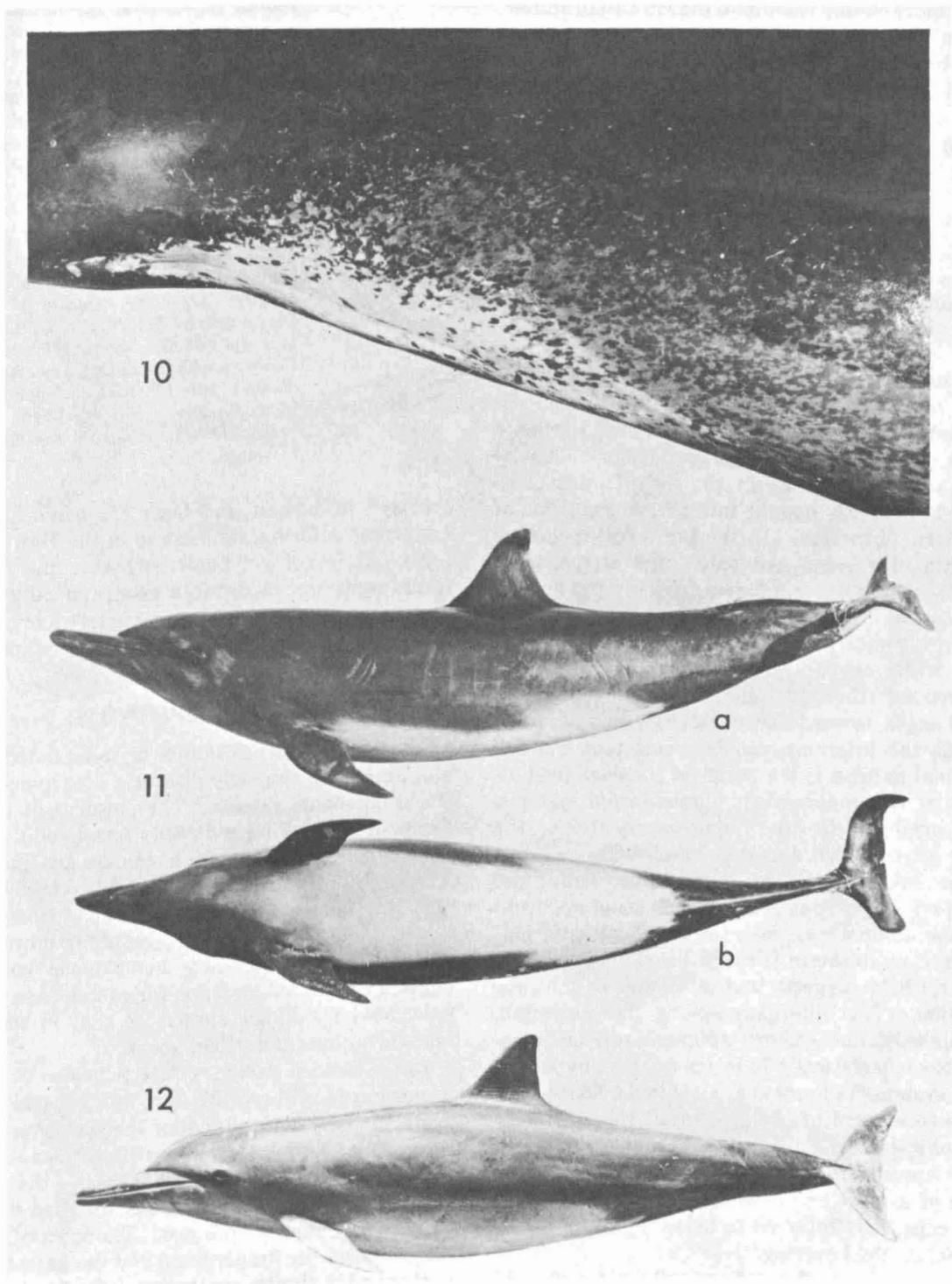
FIGURE 12.—Subadult whitebelly spinner. Female, 129 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP58; U.S. National Museum 396036 (complete skeleton). Photographed after frozen for several months and thawed in water.

convex smooth curve over the eye in the whitebelly spinner but dips over the eye in the Hawaiian form.

The differences among the whitebelly, eastern, and Hawaiian spinners are summarized in Table 1. These differences appear to be based primarily in differential development. The small subadult of the whitebelly spinner (Figures 12 and

TABLE 1.—Summary of some external features differing between adults of Hawaiian, whitebelly, and eastern spinner porpoise.

Feature	Hawaiian spinner	Whitebelly spinner	Eastern spinner
Contrast of cape with lateral field	Very pronounced	Clearly discernible	Effectively absent
Ventral margin of cape over eye	Dips	Smooth curve, no dip	Obscure
Ventral white field	Extends dorsad nearly to level of eye; margin smooth	Extends dorsad variably nearly to level of eye; margin speckled; genital and axillary areas confluent	Restricted to discrete genital and axillary areas of varying extent; margins speckled
Black snout tip	Present	Variable	Absent
Contrast between flipper band and gular region	High	High to medium	Low
Spots in gular region	Absent	Variable	Variable
Flippers	Dark	Dark or speckled	Dark
Dorsal fin in adult male	Falcate	Falcate to triangular	Triangular to canted
Protuberant ventral keel in adult male	Absent	Small to medium	Small to large



13) more closely resembles the Hawaiian spinner than does the adult, in that the margin of the ventral white field is relatively smooth. The pattern of the fetus of the eastern spinner (Figure 25) is also very close to the Hawaiian pattern, with the tripartite effect of cape, lateral field, and high ventral field being very pronounced. The question of which sort of developmental cline is involved, paedogenesis to the west or gerontogenesis to the east, is however yet an open one and must be settled by consideration of additional lines of morphological and zoogeographic evidence.

Pattern component analysis.—Comparison of the color pattern of a partially albinistic subadult whitebelly spinner (Figure 14) with that of a normally pigmented individual of the same sex and nearly the same length (Figure 13) affords insight into the mechanisms of pattern formation. In the lighter-than-normal animal, the cape, eye patch and stripe, gape mark, dorsal fin, and flukes are as in the normal specimen. The lateral field, flipper band, and oblique genital mark are obscure, and the flippers are white on both surfaces. White brushings sweep up from the edge of the cape at about midlength toward the dorsal fin. From these facts, the inference can be made that the full normal pattern is the result of the combined effect of two independent pigmentation systems, one involving the cape and accessory stripes, eye and gape marks, dorsal fin, and flukes, and the other involving lateral field, flipper band, and flippers. While the genital mark is not apparent in the albinistic animal, the developmental pattern of obliteration through development of the lateral field suggests that it belongs to the cape system. The difference among the Hawaiian, whitebelly, and eastern spinners can be interpreted schematically in terms of these hypothetical systems (Figure 26), allowing a clearer picture to emerge of the possible patterns of geographical variation involved. Since the lateral field appears in this sense to be the lateral portion of a more extensive dorsal field overlaying the cape, it is referred to below as an aspect of a "dorsal field overlay."

Among these three forms, the "dorsal field

FIGURE 13.—Lateral (a), dorsal (b), and ventral (c) views of subadult whitebelly spinner. Male, 164 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP65; U.S. National Museum 396017 (complete skeleton). Rostrum damaged. Photographed after frozen for several months and thawed in water.

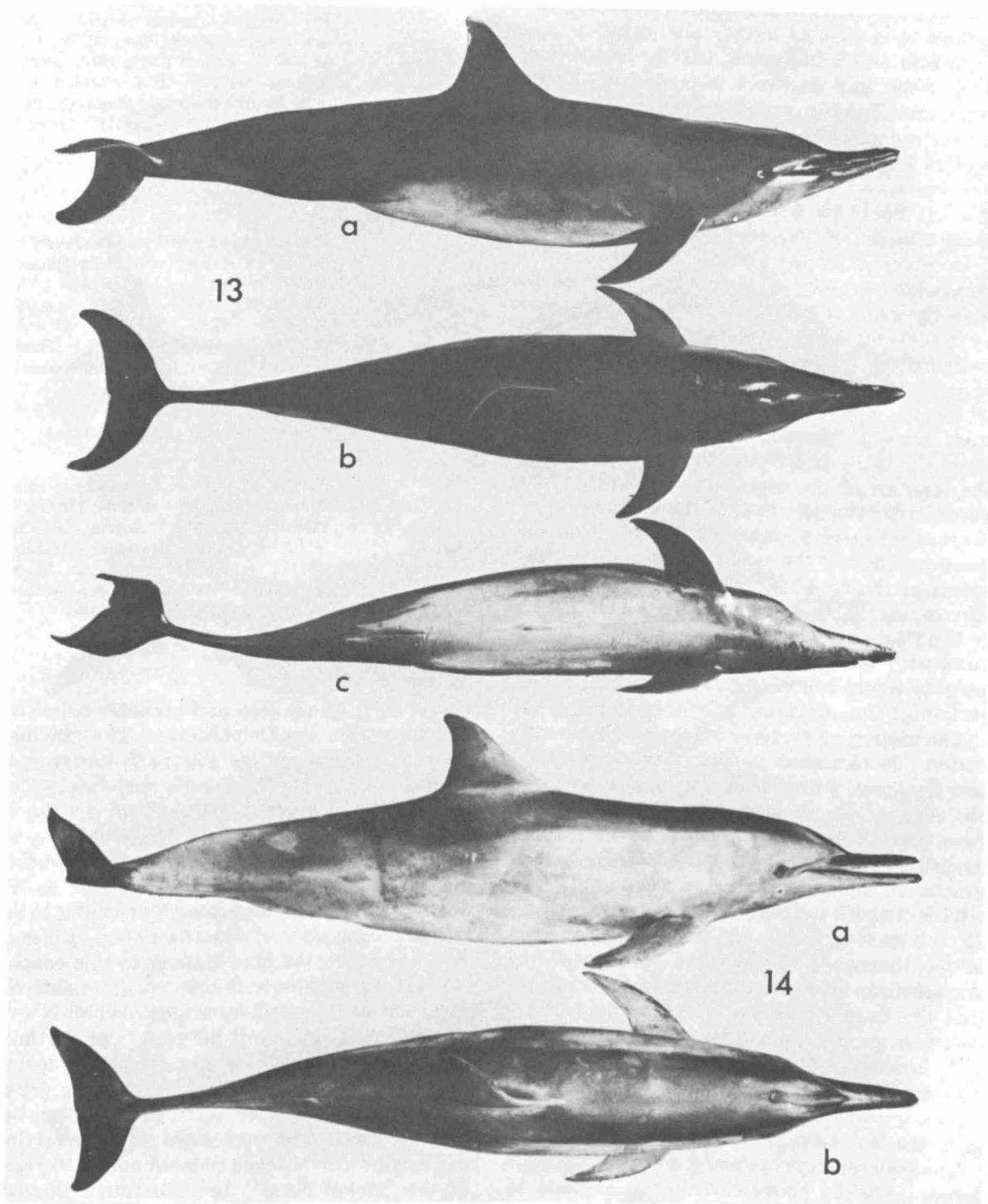
FIGURE 14.—Lateral (a) and dorsal (b) views of albinistic subadult whitebelly spinner. Male, 154 cm, from 10°19'N, 135°38'W, August 5, 1970. Perrin field no. WFP67; U.S. National Museum 396020 (complete skeleton). Compare with normally pigmented animal in Figure 13. Note dark flukes and light flippers. Photographed after frozen for several months and thawed in water.

overlay" is darkest and most extensive in the easternmost form, and least so in the Hawaiian form. It is not yet known whether the three forms represent modes in a geographically continuously varying single species or two or more reproductively isolated allopatric or sympatric populations.

OTHER DELPHINIDS

The color patterns of other closely related delphinids can be similarly dissected into hypothetical component systems. The patterns of three forms of which I have directly examined live or freshly captured dead specimens are analyzed in Figure 27, with an attempt to define possible homologies for the component systems among the species. As the first step in breaking down the patterns into supposedly homologous components, I attempted to define for each a cape with associated markings, similar to that in the albinistic spinner described above.

In the eastern Pacific spotted porpoise, *Stenella graffmani*, (Figure 27, top) the general cape system is very close to that of the spinners, with the cape extending farther ventrad. The dorsal overlay is less extensive than in any of the spinners, and the flipper band runs forward to the gape rather than to the eye. The area of contact between the flipper band and the gape mark in this and in similar spotted porpoise from other



parts of the world is emphasized in many individuals by a zone of lighter pigmentation (see Figures 4 and 6 in Perrin, 1970b; Figure 1 in Best, 1969; and Figure 3 in Nishiwaki, Nakajima, and Kamiya, 1965), which supports the idea of separate origin of the two marks. In the spotted porpoises, the combined pattern systems are overlaid with discrete dorsal and ventral spot systems that to greater or lesser extent obliterate them (Perrin, 1970b).

In *Delphinus* spp. (Figure 27, middle) the dorsal field overlay is less extensive anteriorly than the cape, resulting in invasion of the cape by the ventral field and yielding a four-part criss-cross pattern with zones of black, buff, gray, and white. The deduction to be made is that the whitebelly region represents total lack of pigment, the buff "thoracic patch" (terminology of Mitchell, 1970) represents the color yielded by the pigment of the cape alone, the gray "flank patch" (of Mitchell) that of the pigment of the dorsal field overlay alone, and the black dorsal-most area that of the combined effect of the pigments of the cape and the dorsal field overlay. Chromatographic analysis of pigments present in the various regions and comparison of the results with those of similar tests for other delphinids would contribute to verification or rejection of the suggested homologies.

The pattern of *Tursiops truncatus* (Figure 27, bottom) is very close to that of the spinners in every respect, with the flipper band running to the eye and demarcated dorsally by a narrow light line. The dorsal field overlay of varying darkness extends ventrad to about the same degree as in the eastern spinner. Observation of wild bottlenose porpoise in the eastern temperate and tropical Pacific and examination of some of the thousands of published photographs of animals from around the world lead me to believe that the main component of geographical variation, as for the spinner porpoises, is the extent and darkness of the dorsal overlay. In Hawaiian *Tursiops* that I have observed, the ventral margin was high and sharply defined exactly as in the Hawaiian spinner.

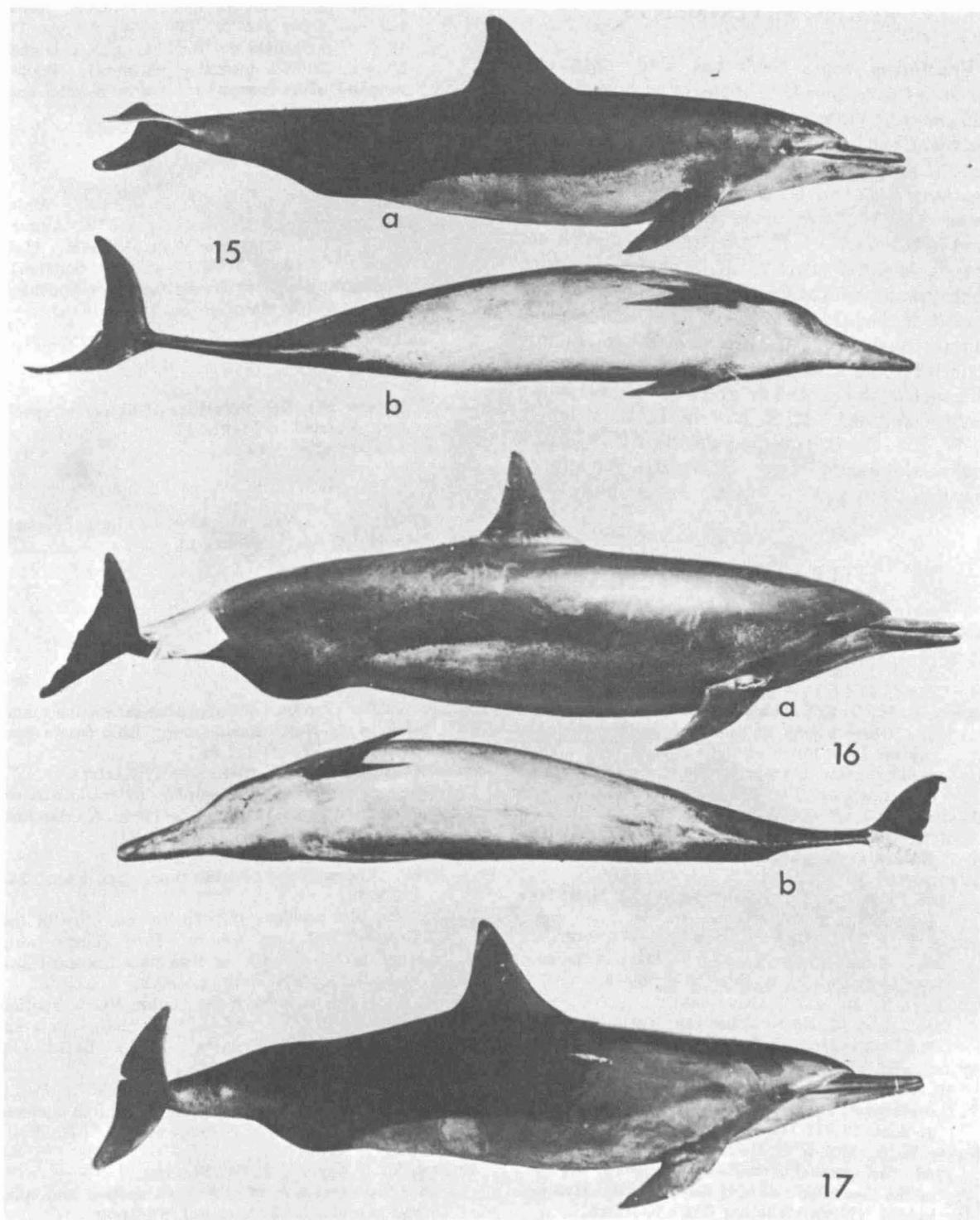
The general cape system common to the four forms discussed above corresponds roughly to the "saddled pattern" described by Mitchell

FIGURE 15.—Lateral (a) and ventral (b) views of subadult whitebelly spinner. Male, 166 cm, from 10°N, 129° or 136°W, August 10-12, 1970. Perrin field no. WFP71; U.S. National Museum 396023 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 16.—Lateral (a) and ventral (b) views of adult whitebelly spinner. Male, 169 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP53; U.S. National Museum 396031 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 17.—Adult whitebelly spinner. Male, 174 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP76; U.S. National Museum 396170 (complete skeleton). Photographed after frozen for several months and thawed in water.

(1970) as a generalized and probably primitive pattern within the Delphinidae. The "saddled pattern" depicted in his Figure 7, however, is definitely not that of the spinner porpoises, which he included in a group of "saddled" species in his Figure 17. I concur with Mitchell in his selection of the "saddled" condition as a good candidate for a primitive pattern, insofar as his definition of that pattern category pertains to the "general cape system" described here. Lines of evidence presented here leading to this conclusion are the possession in common of a relatively invariant cape system by several delphinid species and the tendency of the cape to be partially marked, distorted, or obliterated in a varying fashion within a species or species group not so much by alteration of its intrinsic form but more by interaction with more plastic overlying systems or (as Mitchell pointed out in the case of the "spinal blaze") by subtraction through invasion by areas of nonpigmentation.



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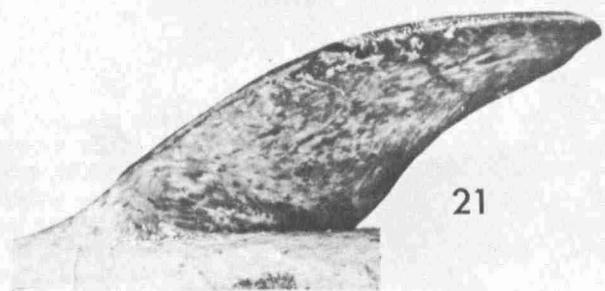
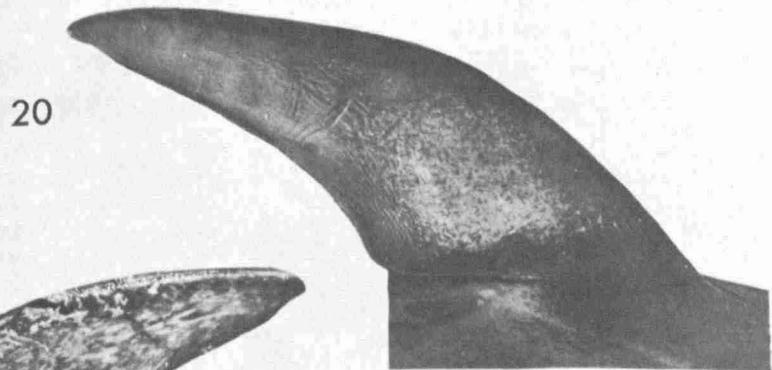
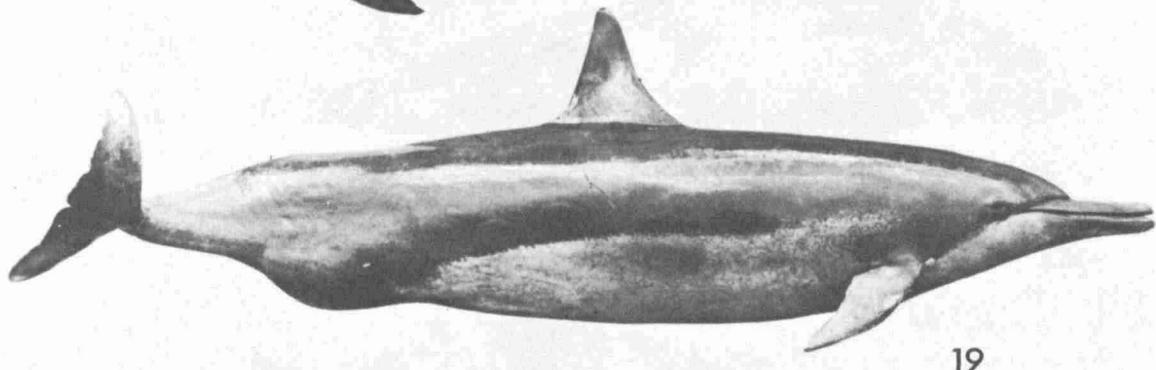
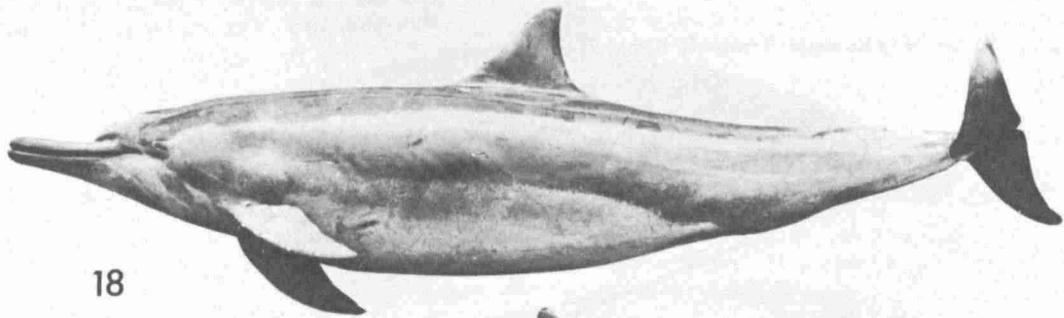
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FIGURE 18.—Adult whitebelly spinner. Male, 177 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP54; U.S. National Museum 396032 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 19.—Adult whitebelly spinner. Male, 178 cm, from 10°N, 128° or 136°W, August 10-12, 1970. Perrin field no. WFP52; U.S. National Museum 396030 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 20.—Dorsal surface of flipper of specimen depicted in Figure 17.

FIGURE 21.—Ventral surface of flipper of specimen depicted in Figure 19.



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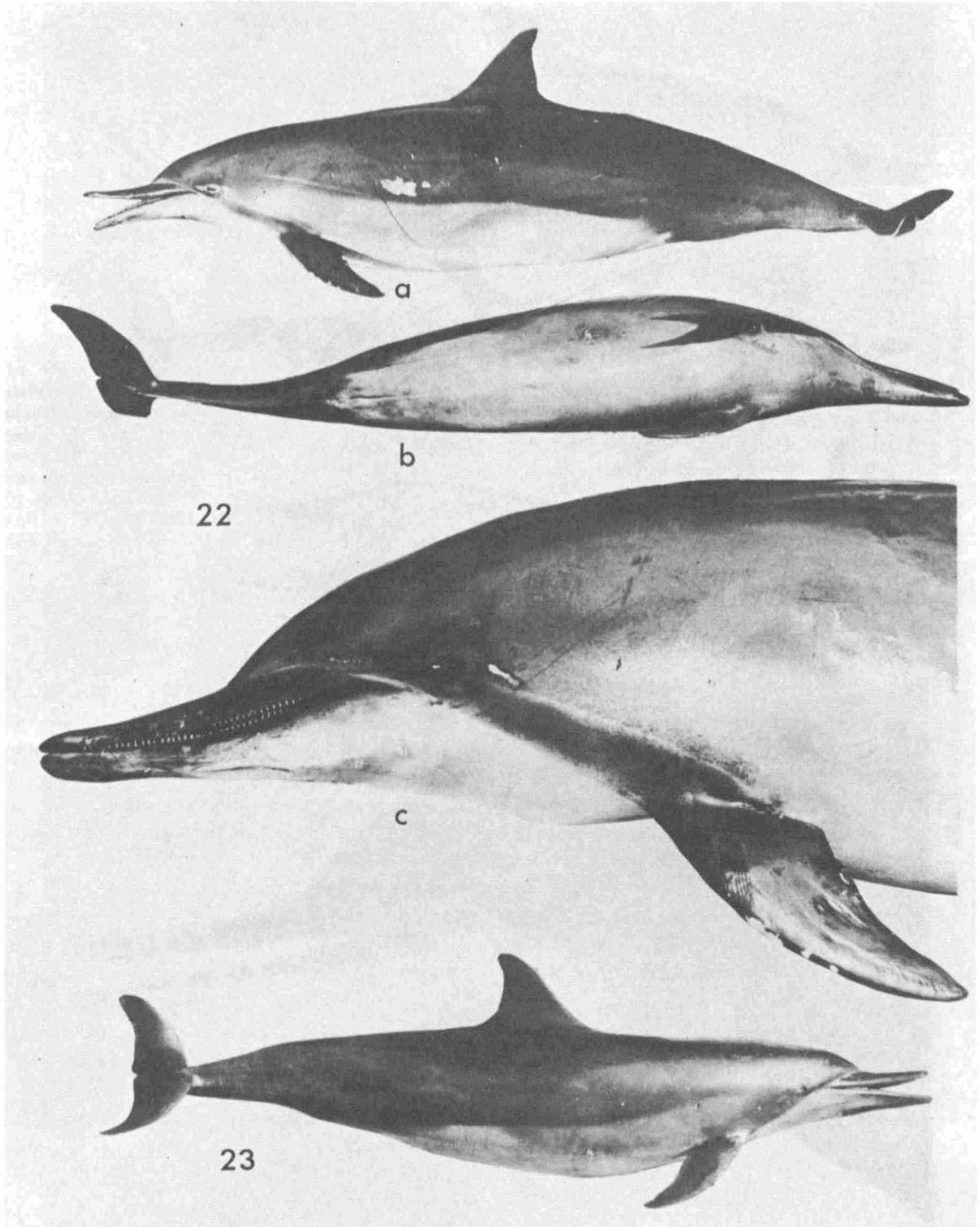
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FIGURE 22.—Lateral (a) and ventral (b) views of adult whitebelly spinner. Female, 179 cm, from 3°20'N, 110°44'W, June 24, 1970. Perrin field no. WFP79; U.S. National Museum 396173 (complete skeleton). Rostrum damaged. Photographed after frozen for several months and thawed in water.

FIGURE 23.—Adult whitebelly spinner. Female, 169 cm, from 8°19'N, 119°15'W or 3°20'N, 110°44'W, June 11 or 24, 1970. Perrin field no. WFP80; U.S. National Museum 396174 (complete skeleton). Photographed after frozen for several months and thawed in water.



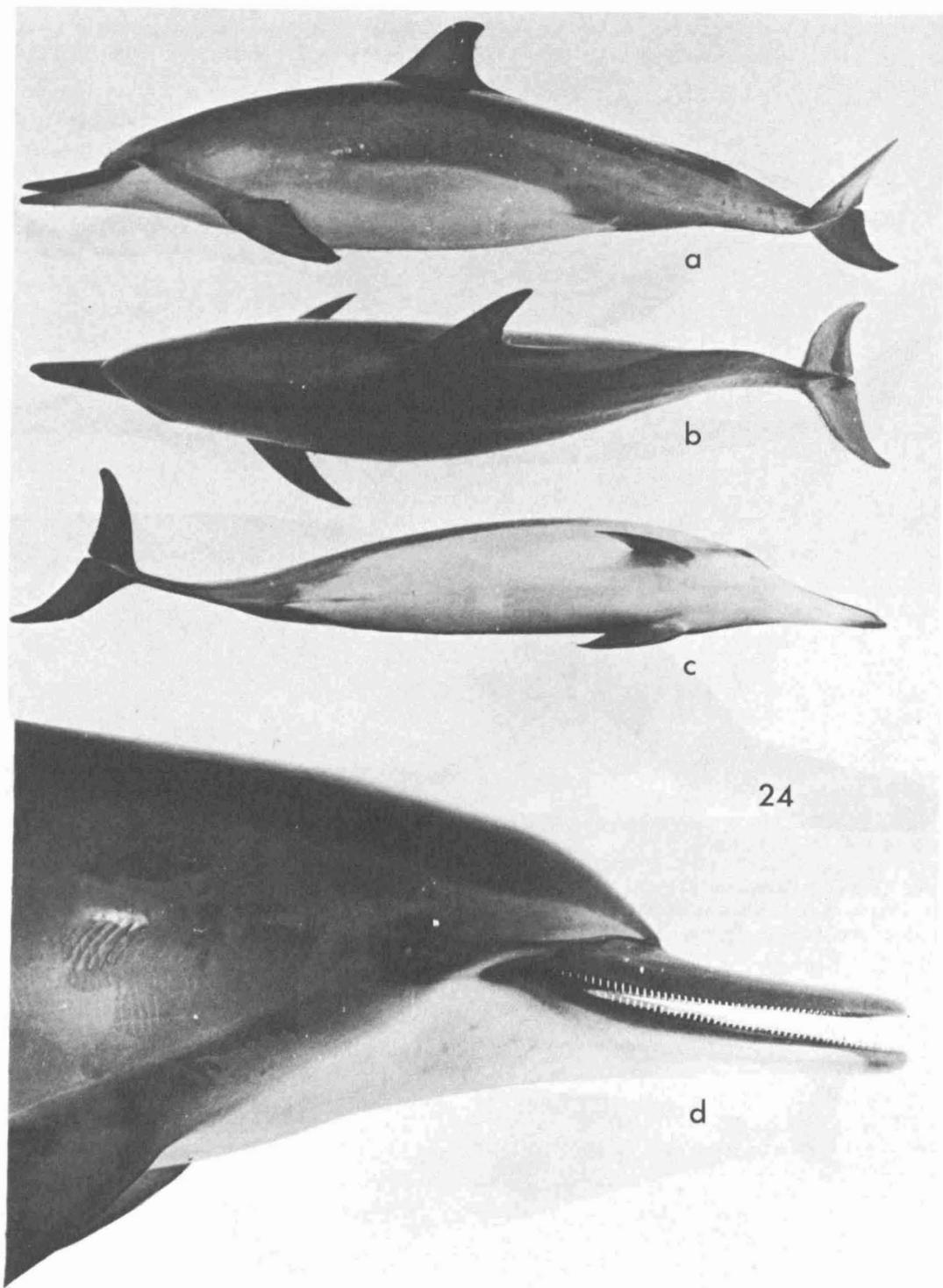


FIGURE 24.—Lateral (a), dorsal (b), ventral (c), and close-up lateral (d) views of Hawaiian spinner porpoise. Subadult male, 179 cm, from Waikiki Beach, Oahu, May 25, 1970. Oceanic Institute field no. OI70-35; specimen stolen during preparation. Photographed 3 hours after death.

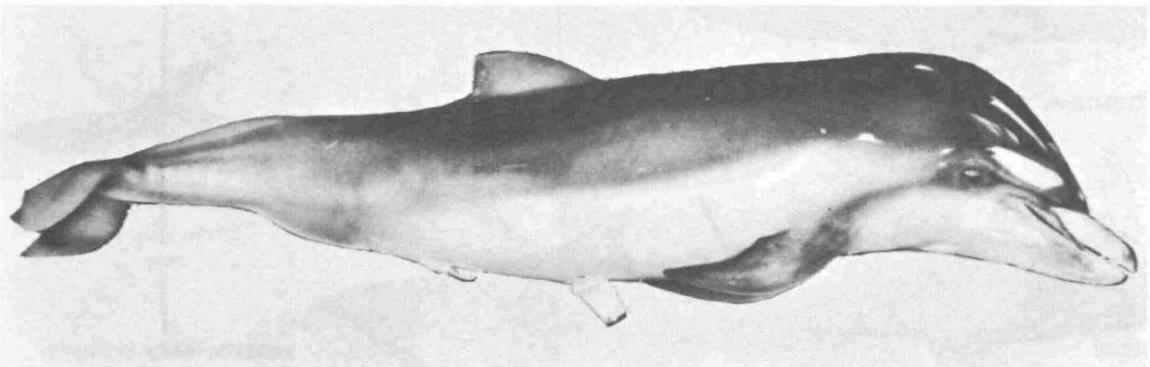


FIGURE 25.—Fetus of eastern spinner. Male, 361 mm, 640 gm, from 9°19'N, 105°20'W, November 10, 1971. Perrin field no. (of mother) WFP187. Specimen at the National Marine Fisheries Service Laboratory, La Jolla, Calif. Photographed underwater after removal from frozen adult, which had been frozen for several months and thawed in water. Dorsal fin folded, and epidermis damaged about head (white areas).

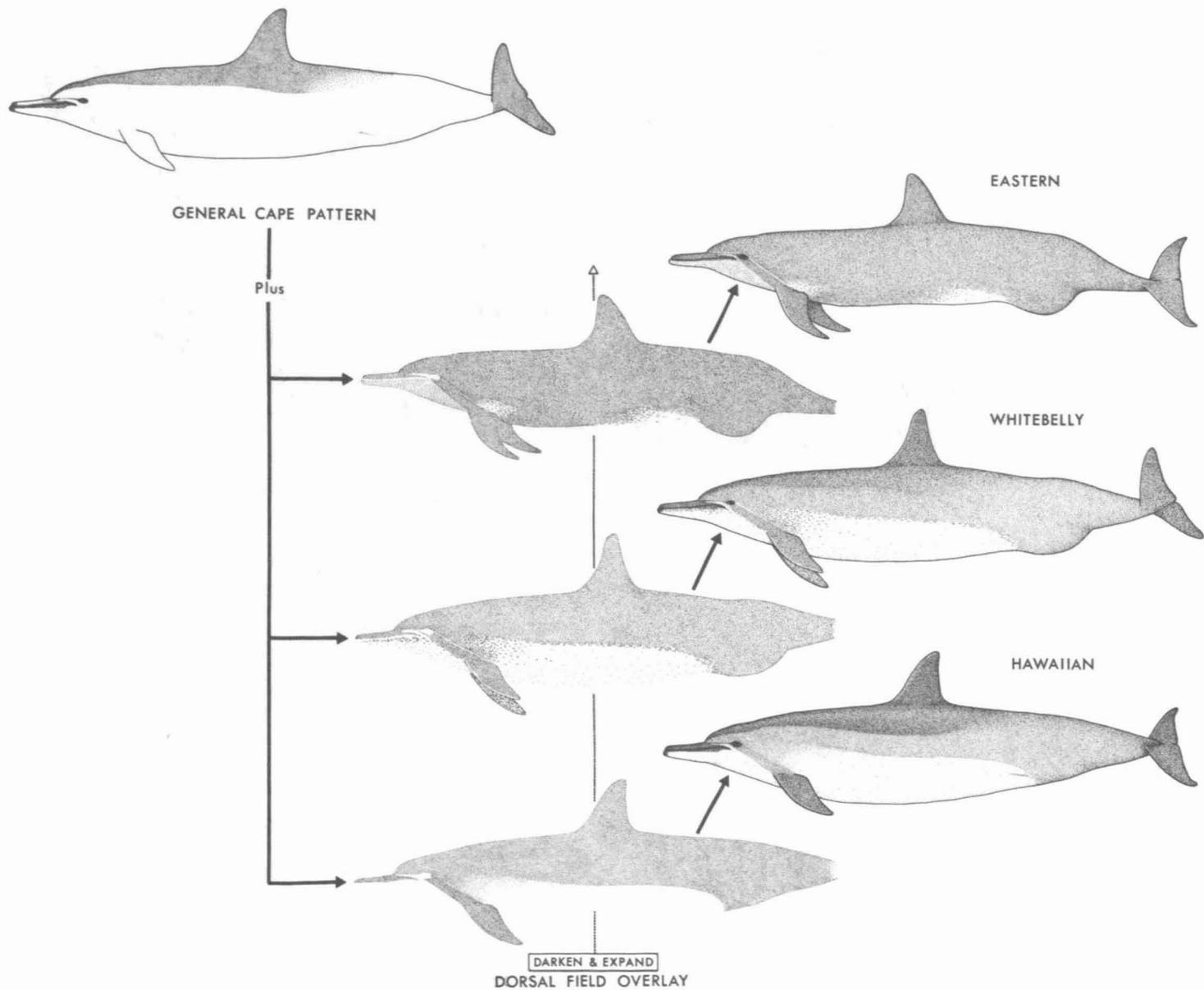


FIGURE 26.—Scheme for analysis of color patterns of spinner porpoises in terms of discrete component systems.

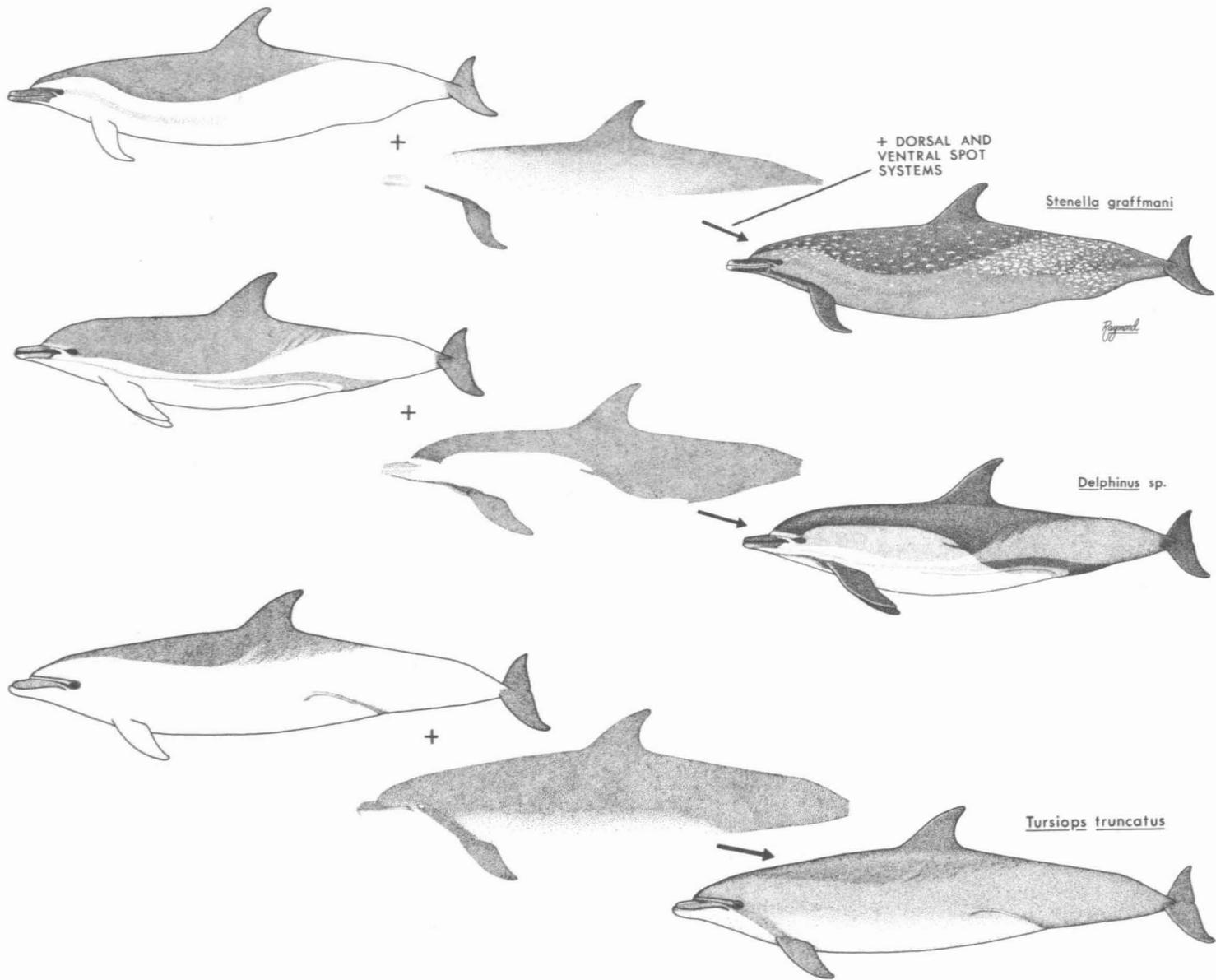


FIGURE 27.—Component analyses of color patterns of *Stenella graffmani*, *Delphinus* sp. (based on observations of specimens taken off southern California), and *Tursiops truncatus* (based on observations of captive specimens from southeast Atlantic coast of United States).